Spectral Effects of Supplemental Greenhouse Radiation on Growth and Flowering of Annual Bedding Plants and Vegetable Transplants

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Additional index words. controlled environments, LEDs, light-emitting diodes, light quality, plant quality, seedlings

Abstract. Supplemental radiation (SR), traditionally provided by high-pressure sodium (HPS) lamps, is recommended for greenhouse production of seedlings during radiation-limiting conditions. Light-emitting diodes (LEDs) have emerged as an appealing alternative to HPS lamps primarily because they can provide SR at improved energy efficiencies, they have longer fixture lifetimes, and the radiation spectrum can be tailored to potentially manipulate plant morphology by targeting radiation absorption of specific photoreceptors. We grew seedlings of three annual bedding plants and two vegetable transplants in greenhouses at 20 °C under a 16-h photoperiod under six SR treatments: five that delivered a photosynthetic photon flux density (PPFD) of 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from HPS lamps (HPS₉₀) or LEDs [four treatments composed of blue (B; 400–500 nm), red (R; 600–700 nm), far red (FR; 700–800 nm), and/or white LEDs] and one that delivered 10 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from HPS (HPS₁₀) lamps as a control with matching photoperiod. The LED treatments, defined by the percentages of B, green (G; 500–600 nm), and R radiation, were B₁₀R₉₀, B₄₅R₅₅, B₁₀G₅R₈₅, and B₁₂G₂₀R₆₈ + FR (FR at 12 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). At transplant, leaf area and seedling height were similar among 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ treatments in all species except snapdragon (*Antirrhinum majus*), in which seedlings grown under B₁₂G₂₀R₆₈ + FR had 62% greater leaf area than those grown under B₄₅R₅₅ and were 47%, 18%, 38%, and 62% taller than those grown under HPS₉₀, B₁₀R₉₀, B₁₀G₅R₈₅, and B₄₅R₅₅, respectively. After transplant and finishing under the same SR treatments, snapdragon flowered on average 7 days earlier under the B₁₂G₂₀R₆₈ + FR treatment than the other LED treatments, whereas geranium (*Pelargonium × hortorum*) grown under B₄₅R₅₅ and B₁₂G₂₀R₆₈ + FR flowered 7 to 9 days earlier than those under the B₁₀G₅R₈₅ and B₁₀R₉₀ treatments. Seedlings of each species grown under the HPS₁₀ treatment accumulated less dry weight and took longer to flower compared with seedlings under the other SR treatments. We conclude that radiation quality of SR has relatively little effect on seedling growth and subsequent flowering although in some crops, flowering may be earlier when SR includes FR radiation.

The photosynthetic daily light integral (DLI) is the cumulative quantity of photons within the photosynthetically active waveband (400–700 nm) incident on a square meter during a 24-h period and is usually

expressed as moles per square meter and day. During commercial seedling production, a minimum DLI of 10–12 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ has been recommended to achieve suitable seedling quality and reduced time to flower after transplant (Lopez and Runkle, 2008; Pramuk and Runkle, 2005). Commercial production of annual (bedding plant and vegetable) seedlings primarily occurs during the winter and early spring, and in the northern United States, the mean outdoor DLI is as low as 5–10 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Korczynski et al., 2002); inside a greenhouse, values are typically 30% to 50% lower. Therefore, SR from electric lamps is commonly used by commercial growers to increase the DLI to increase root and shoot growth. Supplemental radiation is typically delivered by conventional high-intensity discharge lamps, most commonly from HPS lamps, and usually operates during cloudy conditions and at night. Light-emitting diodes have increasing potential to be used for SR applications as the technology develops, particularly as their

intensity and efficacy increase and costs decrease (Bourget, 2008; Wallace and Both, 2016).

Unlike conventional lamps and excluding LEDs coated with phosphors, LEDs emit narrow wavebands based on their chip composition and can therefore emit specific wavebands of interest for a range of plant applications (Mitchell et al., 2015). Early focus of LED use in horticulture was on the application of R (600–700 nm) radiation because it is strongly absorbed by chlorophyll extracts and was the first color to become feasible for horticultural radiation (Bula et al., 1991). Growth under R radiation alone in sole-source radiation (SSR) experiments produced plants with elongated hypocotyls and petioles or decreased chlorophyll development, which could be alleviated with the addition of a relatively low flux of B (400–500 nm) radiation (Hoenecke et al., 1992; Tripathy and Brown, 1995). Unlike broad-spectrum radiation sources, the LED spectral output can be tailored to emit only or mostly photosynthetic or photomorphogenic radiation (Morrow, 2008).

Plant growth and development are controlled by photoreceptors that regulate hypocotyl and internode extension, leaf expansion, chlorophyll orientation, and flowering in response to specific wavebands of radiation. For example, the cryptochrome receptors, cry1 and cry2, respond to wavelengths from 390 to 480 nm and regulate stem extension, guard cell opening, anthocyanin accumulation, and, in at least some species, flower induction (Ahmad et al., 2002). In *Arabidopsis*, cryptochromes mediate hypocotyl elongation through B radiation regulation of gibberellic acid metabolism (Zhao et al., 2007). Phytochrome, a family of proteins that primarily absorb R and FR (700–800 nm) radiation, signals shade avoidance and flowering control through gene-regulated control of transcription networks (Folta and Carvalho, 2015). Phytochrome exists in R-absorbing (inactive) and FR-absorbing (active) forms, and the incident radiation quality (particularly the R:FR) establishes a phytochrome photoequilibrium (PPE). In conditions depleted of R radiation, such as under a plant canopy, the PPE becomes low, which signals stem and petiole elongation (Franklin and Whitelam, 2005). With the narrow emission spectra of LEDs, one can target these photoreceptors to potentially control plant morphology, which can influence quality attributes important for commercial production of ornamental and vegetable seedlings.

Early plant experiments with R and FR LEDs and B radiation from blue fluorescent lamps showed that including B or FR radiation in SSR studies could affect plant morphology, increase plant growth, or both. Brown et al. (1995) grew 21-d-old pepper (*Capsicum annuum* ‘Hungarian Wax’) seedlings under SSR from metal halide lamps, only R radiation from R LEDs (peak = 660 nm), 1% blue fluorescent + 99% R LEDs, and R LEDs + 59 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from FR LEDs (peak = 735 nm), each providing a PPFD

Received for publication 19 May 2017. Accepted for publication 13 July 2017.

This work was supported by the USDA National Institute of Food and Agriculture, Hatch project 192266.

We gratefully acknowledge support by the USDA National Institute of Food and Agriculture’s Specialty Crop Research Initiative, the USDA-ARS Floriculture and Nursery Research Initiative, C. Raker and Sons for donation of plant material, Philips for donation of LED fixtures, and Nate DuRussel for technical assistance. We also thank Jennifer Boldt and Ryan Warner for their critical review of this manuscript.

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of 300 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 12 h·d⁻¹. Plants grown under R + B from fluorescent lamps were shorter than those grown under R radiation alone, whereas those grown under R + FR radiation were tallest. Plants grown without B radiation had negatively affected leaf expansion and dry weight accumulation. In wheat (*Triticum aestivum*) grown under R LEDs (peak = 660 nm) at 350 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 24 h·d⁻¹, adding 10% B radiation increased plant growth and seed quantity, resulting in plants that were comparable with those grown under white fluorescent lamps (Goins et al., 1997).

Far red LEDs have been used in plant applications to manipulate extension growth of leaves and stems, as well as regulate flowering of at least some long-day plants. For example, by adding FR to B and R SSR treatments from LEDs, Park and Runkle (2017) were able to increase photosynthesis in seedlings of four annual bedding plants; those grown under increasing amounts of FR radiation displayed greater leaf expansion that subsequently increased radiation capture. In addition, stem length of tomato (*Solanum lycopersicum*) rootstock seedlings increased from an end-of-day FR radiation treatment from LEDs (Chia and Kubota, 2010). Red + FR radiation has been provided by incandescent bulbs to promote flowering in long-day plants, and R + white + FR LEDs effectively promoted flowering while consuming less energy (Meng and Runkle, 2014). By adding FR radiation from LEDs, it is possible to accelerate flowering of some long-day plants that are FR-radiation sensitive.

High-quality seedlings suitable for shipping and transplanting should have a high dry weight per internode and be compact. Randall and Lopez (2014) reported decreases in seedling height of six ornamental species grown under 15% B + 85% R radiation from LEDs compared with those grown under HPS SR at a PPFD of 160 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. However, the same species grown under 30% B + 70% R LED SR had a height similar to that of those grown under 15% B + 85% R LED SR. Similarly, previous results of growing annual seedlings under LED SR treatments (with 10% to 20% B radiation) showed inconsistent or limited effects on seedling height, leaf area, and dry weight among HPS and LED treatments that delivered the same PPFD (Poel and Runkle, 2017). Providing SR with a greater percentage of B radiation, the addition of FR radiation, and longer treatment periods (from seedling emergence to flowering) could lead to greater differences in growth and development. Therefore, our objective was to evaluate SR from HPS or LEDs (with increased B or added FR radiation) on seedling quality and plant performance after transplant until flowering.

Materials and Methods

Plant material. Seeds of geranium (*Pelargonium xhortorum* 'Pinto Premium Salmon'), pepper 'Long Red Slim Cayenne', petunia (*Petunia xhybrida* 'Single Dreams White'),

snapdragon 'Montego Yellow', and tomato 'Supersweet' were sown into 128-cell plug trays (2.7 × 2.7 cm; 12.0-mL volume) at a commercial greenhouse (C. Raker and Sons, Inc., Litchfield, MI) and delivered to the Plant Science Research Greenhouses at Michigan State University (East Lansing, MI) 4 (replication 1) or 5 d (replication 2) after seeds were sown. For each species, six 128-cell trays were cut in half and the 12 half trays were randomly assigned to six radiation treatments in adjacent greenhouse sections. Seedling trays of each species were placed at about the same position in each section and rotated systematically every 2 d to minimize positional effects within each treatment. Seedlings were irrigated as necessary with water-soluble fertilizer providing (in mg·L⁻¹) 60 N, 23 P, 60 K, 27.7 Ca, 4.6 Mg, 1.3 Fe, 0.6 Mn, 0.6 Zn, 0.6 Cu, 0.4 B, and 0.1 Mo (MSU Plug Special; GreenCare Fertilizers, Inc., Kankakee, IL).

Radiation treatments. Different SR treatments were delivered to each greenhouse section continuously for 16 h·d⁻¹ (0600 to 2200 HR) at a PPFD of 90 ± 10 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (five sections) or 10 ± 2 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (one section) as measured at plant height in nine different horizontal positions by a portable spectroradiometer (PS-200; StellarNet Inc., Tampa, FL) (Fig. 1). Two of the SR treatments were delivered by HPS lamps using either one 150-W fixture (LU150; Acuity Lithonia Lighting, Conyers, GA) or four 400-W fixtures (LR48877; P.L. Light Systems, Beamsville, ON, Canada) to deliver a target PPFD of 10 (HPS₁₀) or 90 (HPS₉₀) $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. The four remaining SR treatments were delivered by commercial 200-W LED fixtures that contained R (peak = 660 nm), B (peak = 453 nm), white (which was the source of G radiation), or FR (peak = 737 nm) LEDs, three of which were wrapped in a layer of flexible, neutral-density mesh (general-purpose aluminum; New York Wire, Grand Island, NY) to reduce radiation intensity by ≈35% without affecting SR spectral output or incident solar radiation. Each LED fixture was mounted horizontally 1.9 m above the bench height, and the 400- and 150-W HPS fixtures were mounted 1.3 and 2.5 m above the plants, respectively. Glass walls between greenhouse sections were coated with a heavy layer of whitewash to prevent radiation treatment contamination.

The four LED treatments were defined by their 100-nm waveband ratios of B, G (500–600 nm), and R radiation (subscript values indicate the percentage of each waveband) and were B₁₀R₉₀, B₄₅R₅₅, B₁₀G₅R₈₅, and B₁₂G₂₀R₆₈ + FR. The B₁₀R₉₀ and B₁₀G₅R₈₅ treatments were delivered by top-lighting fixtures (GP-TOPlight DR/B-LB2013 and GP-TOPlight DR/W-MB2013; Philips, Eindhoven, the Netherlands). The B₄₅R₅₅ treatment was delivered by top-lighting fixtures providing 20% B + 80% R radiation (GP-TOPlight DR/B-HB2013; Philips) with two layers of neutral-density mesh to reduce radiation intensity (by ≈57%), along with 18 B-emitting LED research modules (GreenPower LED

Fig. 1. The relative spectral distributions and estimated phytochrome photoequilibria (PPE) of supplemental radiation treatments between 400 and 800 nm from high-pressure sodium (HPS) and light-emitting diodes delivering different percentages (denoted in subscript) of blue (B; 400–500 nm), green (G; 500–600 nm), red (R; 600–700 nm), and far red (FR; 700–800 nm) radiation.

research module blue; Philips) hung 60 cm above the benches to provide the target PPFD. The fourth LED treatment, B₁₂G₂₀R₆₈ + FR, was provided by top-lighting fixtures that emitted FR radiation at 12 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (GP-TOPlight DR/W/FR_2-HB2013; Philips) and did not require mesh to obtain the target PPFD. The estimated PPE established under each treatment was calculated with spectroradiometer software (SpectraWiz; StellarNet Inc.) that used the formula described by Sager et al. (1988) and ranged from 0.84 to 0.88 (Fig. 1).

Environmental conditions. The experiment was performed in six glass-glazed greenhouse sections oriented west to east and measuring 4.0 m by 4.6 m, with a 2.2-m-high gutter and 3.5-m peak. The set point for air temperature was 20 °C during the day and night, and was maintained by steam heating, exhaust fans, and roof vents controlled by a greenhouse environmental control system (Integro 725; Priva North America, Vine-land, ON, Canada). In each section, air temperature was recorded by an aspirated thermocouple (Type E; Omega Engineering, Stamford, CT) above canopy height. Leaf surface temperature was measured by an infrared thermocouple (Type K, OS36-01; Omega Engineering) placed 15 cm above one seedling tray in each section during the

Table 1. Means ($\pm$ SD) of temperature and photosynthetic daily light integral (DLI) as measured in greenhouses by aspirated thermocouples, infrared sensors, and quantum sensors during the seedling phase under ambient radiation, with supplemental radiation treatments delivered by high-pressure sodium (HPS) lamps or light-emitting diodes (LEDs). For the LED treatments (all delivered at $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), subscript values that follow each waveband of blue (B; 400–500 nm), green (G; 500–600 nm), red (R; 600–700 nm), and far red (FR; 700–800 nm) radiation indicate their percentages. Numbers in subscript after HPS treatments denote their intensity ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

Treatment initiation	Supplemental radiation treatment	Daytime air temp ($^{\circ}\text{C}$)	Daytime canopy temp ($^{\circ}\text{C}$)	Air–canopy temp ($^{\circ}\text{C}$)	DLI ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)
4 Nov.	HPS ₁₀	19.2 $\pm$ 0.9	14.0 $\pm$ 2.6	5.2	3.8 $\pm$ 1.7
	HPS ₉₀	19.5 $\pm$ 1.2	17.2 $\pm$ 3.3	2.3	7.0 $\pm$ 1.7
	B ₁₀ R ₉₀	19.4 $\pm$ 1.0	15.9 $\pm$ 2.9	3.4	7.3 $\pm$ 1.6
	B ₁₀ G ₅ R ₈₅	20.0 $\pm$ 0.6	17.1 $\pm$ 2.9	2.8	7.6 $\pm$ 1.6
	B ₁₂ G ₂₀ R ₆₈ + FR	19.5 $\pm$ 0.9	16.2 $\pm$ 2.1	3.3	7.2 $\pm$ 1.6
	B ₄₅ R ₅₅	20.4 $\pm$ 1.5	18.1 $\pm$ 2.3	2.3	6.7 $\pm$ 1.5
29 Dec.	HPS ₁₀	19.0 $\pm$ 0.7	11.5 $\pm$ 3.1	7.5	3.5 $\pm$ 1.2
	HPS ₉₀	19.7 $\pm$ 1.1	15.3 $\pm$ 2.5	4.4	7.7 $\pm$ 1.0
	B ₁₀ R ₉₀	18.8 $\pm$ 0.9	14.3 $\pm$ 2.0	4.5	7.7 $\pm$ 0.9
	B ₁₀ G ₅ R ₈₅	18.8 $\pm$ 1.5	13.2 $\pm$ 1.8	5.6	8.7 $\pm$ 1.1
	B ₁₂ G ₂₀ R ₆₈ + FR	19.7 $\pm$ 0.8	14.7 $\pm$ 1.9	5.1	7.2 $\pm$ 1.0
	B ₄₅ R ₅₅	20.7 $\pm$ 0.8	12.1 $\pm$ 1.9	8.5	7.2 $\pm$ 0.9

Table 2. Means ($\pm$ SD) of temperature and photosynthetic daily light integral (DLI) as measured in greenhouses by aspirated thermocouples, infrared sensors, and quantum sensors from transplant to flowering under ambient radiation, with supplemental radiation treatments delivered by high-pressure sodium (HPS) lamps or light-emitting diodes (LEDs). For the LED treatments (all delivered at $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), subscript values that follow each waveband of blue (B; 400–500 nm), green (G; 500–600 nm), red (R; 600–700 nm), and far red (FR; 700–800 nm) radiation indicate their percentages. Numbers in subscript after HPS treatments denote their intensity ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$).

Transplant date	Supplemental radiation treatment	Daytime air temp ($^{\circ}\text{C}$)	Daytime canopy temp ($^{\circ}\text{C}$)	Air–canopy temp ($^{\circ}\text{C}$)	DLI ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)
25 Nov.	HPS ₁₀	19.0 $\pm$ 0.7	13.3 $\pm$ 1.1	5.6	3.5 $\pm$ 1.4
	HPS ₉₀	19.8 $\pm$ 1.3	16.7 $\pm$ 3.1	3.2	7.6 $\pm$ 1.1
	B ₁₀ R ₉₀	19.2 $\pm$ 1.0	16.0 $\pm$ 2.8	3.1	7.6 $\pm$ 1.1
	B ₁₀ G ₅ R ₈₅	18.9 $\pm$ 0.9	15.4 $\pm$ 3.4	3.5	8.4 $\pm$ 1.5
	B ₁₂ G ₂₀ R ₆₈ + FR	19.8 $\pm$ 0.9	16.2 $\pm$ 2.7	3.6	7.4 $\pm$ 1.1
	B ₄₅ R ₅₅	20.6 $\pm$ 0.8	13.7 $\pm$ 3.1	6.9	7.3 $\pm$ 1.0
20 Jan.	HPS ₁₀	19.8 $\pm$ 1.4	15.2 $\pm$ 2.9	4.6	5.6 $\pm$ 2.3
	HPS ₉₀	20.7 $\pm$ 1.7	21.1 $\pm$ 5.2	–0.4	9.1 $\pm$ 1.9
	B ₁₀ R ₉₀	19.7 $\pm$ 1.2	18.9 $\pm$ 3.4	0.7	9.6 $\pm$ 1.9
	B ₁₀ G ₅ R ₈₅	19.0 $\pm$ 1.2	16.6 $\pm$ 4.2	2.4	10.4 $\pm$ 1.7
	B ₁₂ G ₂₀ R ₆₈ + FR	20.4 $\pm$ 1.2	17.8 $\pm$ 4.2	2.6	9.3 $\pm$ 1.9
	B ₄₅ R ₅₅	21.4 $\pm$ 1.0	14.7 $\pm$ 3.7	6.7	9.2 $\pm$ 1.8

seedling phase and 5 cm above one plant during the transplant phase and oriented downward at a 45° angle. The *PPFD* was measured in each treatment at bench height and recorded by a quantum sensor (LI-190SA; LI-COR, Lincoln, NE). Whitewash (Kool Ray Classic; Continental Products Co., Euclid, OH) was applied on the glass-glazed greenhouse exterior to decrease the intensity (by $\approx 20\%$) midway through the second replication. Environmental conditions in each section were monitored and logged with a data logger (CR-10; Campbell Scientific, Logan, UT) every 10 s, and hourly averages were recorded. Environmental data during the seedling and transplant phases are reported in Tables 1 and 2, respectively.

Seedling measurements and transplant. After 14–26 d of radiation treatments (depending on species and seasonal conditions), eight seedlings from each block, 16 seedlings in total, were sampled at random, excluding those in edge rows, and the following measurements were made: leaf area [using a leaf area meter (LI-3000; LI-COR)], leaf number (those $\geq 1 \text{ cm}^2$), and plant height (from substrate surface). Shoots were cut at the medium surface, and roots, separated from the medium in a washbasin, were then

Fig. 2. Plant height of five seedling crops grown under ambient greenhouse radiation and supplemental lighting from two high-pressure sodium (HPS) or four light-emitting diode (LED) treatments delivering different percentages of blue (B; 400–500 nm), green (G; 500–600 nm), red (R; 600–700 nm), and far red (FR; 700–800 nm) radiation. All treatments delivered a photosynthetic photon flux density of $90 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, except HPS₁₀, which delivered $10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. For the LED treatments, subscript values denote the waveband proportions. NS = nonsignificant; means sharing a letter are not statistically different by Tukey's honest significant difference test at $P \leq 0.05$. Error bars indicate standard error.

Fig. 3. The leaf number and leaf area of five seedling crops grown under ambient greenhouse radiation and supplemental radiation from two high-pressure sodium (HPS) or four light-emitting diode treatments delivering different percentages of blue (B; 400–500 nm), green (G; 500–600 nm), red (R; 600–700 nm), and far red (FR; 700–800 nm) radiation. See caption for Fig. 2 for treatment and statistical information.

placed in paper envelopes and into a drying oven (NAPCO 630; NAPCO Scientific Co., Tualatin, OR) at 80 °C for at least 48 h then measured for shoot and root dry weight. From the remaining seedlings, 10 each (five from each block) of geranium, petunia, and snapdragon from each treatment were transplanted into 10-cm pots containing 70% peatmoss, 21% perlite, and 9% vermiculite (SUREMIX; Michigan Grower Products Inc., Galesburg, MI) and returned to their respective SR treatment. Pots were irrigated with line-fed water-soluble fertilizer providing (in mg·L⁻¹) 125 N, 12 P, 100 K, 65 Ca, 12 Mg, 1 Fe and Cu, 0.5 Mn and Zn, 0.3 B, and 0.1 Mo (MSU RO Water Special; GreenCare Fertilizers, Inc.) as necessary and rotated positionally every 2 d. Date of first open flower or inflorescence, height at first

flower (measured from the media surface to the tallest leaf for geranium and shoot tip for petunia and snapdragon), and the total number of open flowers for petunia or inflorescences with open flowers for geranium and snapdragon, 7–10 d after flowering, were recorded.

Experimental design and data analysis. The experiment was performed twice, with seed sowings in Nov. and Dec. 2015. Data were analyzed as a randomized complete block design with subsamples to account for seasonal changes in DLI and temperature, among other factors. Data were analyzed with the mixed-model procedure (PROC MIXED) in SAS 9.4 (SAS Institute, Cary, NC), and pairwise comparisons between treatments were performed with Tukey's honest significant difference test ($P \leq 0.05$).

Results

Seedling height. At transplant, seedlings of petunia, snapdragon, tomato, and pepper were shorter when grown under the HPS₁₀ treatment compared with those grown under HPS₉₀; height of geranium seedlings was similar under all treatments (Fig. 2). Tomato, pepper, and petunia seedlings grown under any 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatment were similar in height; however, petunia seedlings grown under B₄₅R₅₅ were similar in height to those grown under HPS₁₀ SR. Snapdragon seedlings grown under B₁₂G₂₀R₆₈ + FR were the tallest among treatments, followed by those grown under B₁₀R₉₀, and those under the remaining 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments were similar in height.

Leaf number and leaf area of seedlings. Tomato seedlings grown under B₄₅R₅₅ had more leaves at transplant than those grown under B₁₀R₉₀, B₁₀G₅R₈₅, and HPS₁₀ SR, whereas those under each of the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments had more leaves than those grown under HPS₁₀ (Fig. 3). There were no other differences in leaf number among the other crops grown under the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments. The total leaf area for all crops studied was similar among the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments except for snapdragon seedlings, in which those grown under B₄₅R₅₅ had 37% less leaf area than seedlings grown under B₁₂G₂₀R₆₈ + FR. Leaf area under HPS₁₀ SR was 63%, 64%, 64%, and 75% less than that of seedlings grown under HPS₉₀ SR in pepper, tomato, snapdragon, and petunia, respectively. There were no differences in average leaf area (the quotient of total leaf area and average leaf number) among 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments (data not presented).

Seedling dry weights. In all crops tested, dry shoot weight was significantly less in seedlings grown under the HPS₁₀ treatment than those grown under the LED and HPS₉₀ SR treatments (Fig. 4). Seedlings grown under HPS₁₀ accumulated 53%, 68%, 69%, 75%, and 79% less dry weight in geranium, pepper, tomato, petunia, and snapdragon, respectively, compared with those grown under HPS₉₀. Among the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments, only pepper seedlings exhibited a difference in dry weight among LED SR treatments: those under B₁₀R₉₀ SR accumulated less dry matter than seedlings grown under HPS₉₀ SR.

Root dry weights of tomato, petunia, pepper, and snapdragon were 40%, 57%, 68%, and 76% less, respectively, when grown under HPS₁₀ than those grown under HPS₉₀ SR. Tomato seedling root weight was greater under HPS₉₀ SR and B₁₂G₂₀R₆₈ + FR LED SR compared with that in the HPS₁₀ treatment, whereas weights under the remaining LED SR treatments were similar. In all crops tested, there were no differences in dry root weights among the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments.

Days to first flower. Seedlings grown under HPS₁₀ continuously (during the seedling and transplant phases) took the longest to

Fig. 4. Dry shoot and root weights of five seedling crops grown under ambient greenhouse radiation and supplemental radiation from two high-pressure sodium (HPS) or four light-emitting diode treatments delivering different percentages of blue (B; 400–500 nm), green (G; 500–600 nm), red (R; 600–700 nm), and far red (FR; 700–800 nm) radiation. See caption for Fig. 2 for treatment and statistical information.

flower (Fig. 5). On average, snapdragon, petunia, and geranium under the HPS₁₀ treatment flowered 19, 23, and 24 d later than those grown under the HPS₉₀ treatment. Petunia transplants grown under 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments took a similar number of days to flower, whereas among LED SR treatments, snapdragon flowered earliest when grown under the B₁₂G₂₀R₆₈ + FR treatment. Geranium transplants grown under B₁₀R₉₀ and B₁₀G₅R₈₅ took longer to flower than those grown under B₁₂G₂₀R₆₈ + FR and B₄₅R₅₅, but flowering time was similar to that of plants grown under HPS₉₀.

Plant height at first flower. Snapdragon plants were of similar height at flowering under all SR treatments. Petunia plants grown under HPS₁₀ were taller at first flower than those grown under HPS₉₀, B₁₀R₉₀, and B₄₅R₅₅, but their height was similar to that of those grown under B₁₀G₅R₈₅ and B₁₂G₂₀R₆₈ + FR.

Petunia grown under B₁₀R₉₀ were shorter at first flower than those grown under B₁₂G₂₀R₆₈ + FR, but were of similar height to those grown under the remaining treatments. Geranium was shorter at first flower when grown under the B₄₅R₅₅ treatment compared with those under the HPS₁₀, HPS₉₀, and B₁₂G₂₀R₆₈ + FR treatments.

Total flower number. Snapdragon grown under HPS₉₀ and B₁₂G₂₀R₆₈ + FR had more inflorescences (8) than those grown under HPS₁₀ (5), whereas inflorescence number among 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ treatments was similar. Petunia grown under B₁₂G₂₀R₆₈ + FR SR had more flowers (25) than those grown under HPS₁₀ and B₁₀G₅R₈₅ (13 and 12, respectively). Similarly, geranium had the most inflorescences when grown under the B₁₂G₂₀R₆₈ + FR treatment and the least under HPS₁₀ (3 and 1, respectively). The B₁₀R₉₀ treatment was the only 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR

treatment for which the plant inflorescence number was similar to that of those grown under HPS₁₀.

Discussion

One of our objectives was to determine whether SR that emitted a relatively high percentage (45%) of B radiation would inhibit extension growth of seedlings. Previously, we observed little or no effect of radiation quality of SR treatments on seedling growth and morphology when SR emitted 10% to 20% B radiation (Poel and Runkle, 2017). Blue radiation can suppress stem extension and leaf expansion through a cryptochrome-mediated pathway altering gene expression (Folta and Childers, 2008) and perhaps through other B radiation-mediated photoreceptors. For example, Wollaeger and Runkle (2015) grew seedlings of *impatiens walleriana*, *salvia splendens*, petunia, and tomato under LED SSR with six B:R ratios (from 100:0 to 0:100), and as little as 10 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ of B radiation (6.25% of the PPFD) inhibited extension growth, whereas cryptochrome receptors were likely saturated with B radiation at 40 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ because plants receiving more than 25% B radiation were similar in height.

Despite the increased ratio of B radiation in the B₄₅R₅₅ treatment, there were few differences or consistent responses in leaf expansion and plant height under the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ treatments. Snapdragon seedlings grown under B₄₅R₅₅ were 26% and 37% shorter than those grown under B₁₀R₉₀ and B₁₂G₂₀R₆₈ + FR, respectively; however, the addition of FR radiation may be a confounding factor in this second comparison. There were no differences in plant height or leaf area in the other four species tested among the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ treatments. A similar lack of response in stem elongation and leaf expansion was reported under SR with 0% to 16% B radiation delivered with R radiation to tomato (Hernandez and Kubota, 2012), and when cucumber (*Cucumis sativus*) seedlings were grown under a relatively high DLI (16.2 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) (Hernandez and Kubota, 2014). By contrast, seedlings of snapdragon, vinca (*Catharanthus roseus*), impatiens, geranium, petunia, and marigold (*Tagetes patula*) were more compact when grown under LED SR delivering 15% and 30% B radiation with R radiation compared with those grown under HPS, but there were no differences in plant height between the two B + R LED SR treatments (Randall and Lopez, 2014). The lack of a clear B radiation response in our and other SR studies could be attributed to the saturation of B radiation-absorbing photoreceptors (e.g., cryptochrome) from background ambient sunlight. All plants received a DLI of $\approx 3\text{--}5$ $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ from sunlight (Tables 1 and 2), which equates to $\approx 0.7\text{--}1.2$ $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ of B radiation, potentially enough to saturate B radiation photoreceptors across all treatments.

Fig. 5. Days to flower after transplant, plant height at first flower, and total flower or inflorescence number of three seedling crops grown under ambient greenhouse radiation and supplemental radiation from two high-pressure sodium (HPS) or four light-emitting diode treatments delivering different percentages of blue (B; 400–500 nm), green (G; 500–600 nm), red (R; 600–700 nm), and far red (FR; 700–800 nm) radiation. For petunia, the y axis values for flower number are divided by three, as noted. See caption for Fig. 2 for treatment and statistical information.

We were also interested in the effects of SR treatments (especially the different percentages of B radiation) on plant growth after transplant. After 12 weeks under SR, geranium plants grown under B₄₅R₅₅ were 27% shorter at flowering than those grown under HPS₉₀, but were similar to those under the other two LED treatments without FR radiation. Snapdragon were of the same height at flowering under all SR treatments, and petunia plants were generally similar under the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments. In another SR experiment, shoot length of three poinsettia (*Euphorbia pulcherrima*) cultivars after 12 weeks was reduced by 20% to 34% under 20% B + 80% R radiation from LEDs compared with that under HPS lamps (Islam et al., 2012). The authors attributed the reduced plant height to the increased B radiation in the LED treatment and cryptochrome-mediated elongation suppression. The lack of consistent plant height effects in petunia and snapdragon, but shorter geranium at first flower, under the B₄₅R₅₅ treatment could be

attributed to the increased time under the SR treatments; geraniums flowered in an average of 66 d after transplant, whereas petunia and snapdragon flowered in half that time and therefore had shorter exposure to the SR treatments. It is also possible that geranium is more sensitive to B radiation effects, and additional studies focusing on spectral sensitivity compared with other species are needed.

A second experimental objective was to investigate the effect of adding FR to SR on seedling extension growth and subsequent flowering. Through manipulation of the phytochrome photoreceptors, FR radiation can regulate plant growth and flowering. There is generally an inverse linear relationship of PPE to extension growth; however, specific responses to the R:FR ratio vary among species and depend on the inclusion of other wavelengths (Runkle and Heins, 2001). In our study, snapdragon seedlings grown under the FR-emitting SR treatment (PPE = 0.84) were tallest among treatments and had

a greater leaf area than those grown under B₄₅R₅₅ (PPE = 0.86). Park and Runkle (2017) reported up to a 53% increase in snapdragon seedling height and 41% increase in leaf area at transplant as PPE decreased from 0.88 to 0.69 in SSR treatments when the intensity of B radiation was constant. Although the SR treatments had slightly different PPEs, morphological responses could be confounded by the different intensities of B, G, and R radiation delivered in each treatment. The effects of SR on plant height at flowering were inconsistent although plants grown under the B₁₂G₂₀R₆₈ + FR treatment were always at least as tall as those grown under the other LED SR treatments. The commercial fixtures used in this experiment did not have adjustable spectra; therefore, further testing with fixed ratios of B, G, and R radiation among treatments would be needed to isolate the effects from added FR radiation.

In the production of ornamental transplants, producing compact seedlings is a common objective, which can be achieved with radiation with a high R:FR ratio, but a high R:FR ratio can potentially delay flower initiation and development in some long-day plants (Runkle and Heins, 2001). Snapdragon grown under the B₁₂G₂₀R₆₈ + FR treatment flowered 8 d earlier than those under the remaining LED SR treatments although time to flower was similar to that of those under the HPS₉₀ treatment. Under an FR-radiation-intercepting filter creating a high R:FR, flower initiation was delayed in campanula (*Campanula carpatica*) and coreopsis (*Coreopsis grandiflora*), and flower development was inhibited in viola (*Viola xwittrockiana*) (Runkle and Heins, 2001). Runkle and Heins (2003) were successful in promoting flowering of viola by adding FR radiation inside an FR-deficient environment throughout the photoperiod, or for 4 h, at the end of the photoperiod or during the middle of the 15-h night. However, treatments that promoted flowering also promoted extension growth. More experimentation is required to determine the usefulness of including FR radiation in SR on plant growth and development, perhaps with higher FR intensities or alteration of the timing at which it is delivered.

When the ambient solar DLI is low (e.g., <8 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$), SR can be used in greenhouses to increase DLI and thus quality parameters of seedlings (Pramuk and Runkle, 2005). The DLI under the HPS₁₀ treatment was $\approx 3\text{--}4 \text{ mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ lower than under the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments, whereas the photoperiod was the same (16 h). In previous SR experiments that increased DLI during the seedling phase, growth (as measured by dry mass accumulation), stem caliper, and leaf area increased (Hernandez and Kubota, 2014; Randall and Lopez, 2015). For example, Hernandez and Kubota (2014) grew cucumber plants in a greenhouse with and without SR at a PPFD of 54 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ from LEDs at three different R and B radiation ratios at two ambient DLIs, 5.2 and 16.2 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$. At both DLIs, the

seedlings grown with SR had a greater dry and fresh weight, leaf number, leaf area, and stem diameter. Similarly, in our experiment, seedlings of each species had a greater dry shoot weight when grown under the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments. Root dry weight, leaf area, and leaf number were also greater for three of five species grown under SR.

Plants can exhibit shade-avoidance responses, such as increases in extension growth, in response to decreases in the R:FR ratio, the *PPFD*, or both (Ballaré et al., 1991; Smith, 1982). Hernandez and Kubota (2014) reported an increase in hypocotyl length for seedlings grown without SR, but in this current study, seedlings grown under the lower DLI were of the same height as or shorter than those grown under the 90 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ SR treatments. Similarly, seedling height of five species was similar or shorter under ambient radiation compared with that of those grown under SR from HPS lamps or LEDs (Randall and Lopez, 2015). However, in a separate study, stem length of impatiens and salvia decreased as DLI increased, whereas the opposite occurred in marigold and celosia [*Celosia argentea* var. *plumosa* (Pramuk and Runkle, 2005)]. We attribute the shorter seedlings in our study to the development of fewer nodes at transplant. Compared with those grown under HPS₉₀, seedlings of pepper, tomato, petunia, and snapdragon grown under HPS₁₀ were 37%, 44%, 46%, and 62% shorter and had 31%, 44%, 33%, and 31% fewer nodes, respectively. Therefore, a paradigm exists that although plant height increases under low-radiation conditions, plants may be shorter than those grown under higher radiation because they are less mature.

Providing an increased DLI to plants during the finishing stage can decrease time to flower, increase finished plant quality, or both in many species (Blanchard et al., 2011). Therefore, we postulated that time to flower would be reduced by providing SR during the transplant and finishing phases. Faust et al. (2005) reported that increasing DLI from 5 to 19 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ during the transplant phase decreased days to flower for marigold, petunia, salvia, and zinnia. In our experiment, all species tested flowered earlier under the high-intensity SR treatments. Similarly, Sams et al. (2016) noted an increase in the inflorescence number on marigold grown under SR that added 8.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (from HPS lamps or LEDs) to a solar DLI of 11.5 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ compared with those grown without SR. We observed an increase in the inflorescence number in geranium under four SR treatments compared with those grown under HPS₁₀, whereas flower and inflorescence numbers in petunia and snapdragon showed inconsistent responses to DLI. However, more radiation does not necessarily increase the flower number at first flowering. Although an increased DLI decreased time to flower, there was also a decrease in the total flower number at first flowering (Pramuk and Runkle, 2005). Plants that take longer to flower have a longer vegetative phase and

therefore have more time to harvest radiation and accumulate carbohydrates for flower production. A similar response in flower production occurred when plants were grown at lower temperatures; time to flower and the flower number at first flowered generally increased as the average daily temperature decreased (Vaid et al., 2014).

Even with an increased percentage of B radiation in our SR treatments, we were not able to elicit consistent responses in seedling or transplant growth and morphology. Growing geraniums for their complete life cycle under B₄₅R₅₅ SR (with a higher percentage of B radiation) could be an effective tool for height control, depending on the DLI conditions. The inclusion of FR radiation with SR also showed inconsistent responses, but it did accelerate flowering of snapdragon and may have a similar effect on other long-day crops when the natural photoperiod is short. Research with SR treatments with more extreme spectral differences in B and FR radiation or a range of ambient solar DLIs, and perhaps other wavebands, is needed to further explore the potential of how SR can be used to achieve more compact growth and early flowering of ornamental crops.

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